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Principal Investigators: Prof. J. L. Meiry
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Fourth Semi-Annual Status Report
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I. BIOPHYSICS OF THE HUMAN VESTIBULAR SYSTEM

The objective of this research was to evaluate the dynamic characteristics of the human semicircular canals by a detailed examination of their physical properties and to correlate them with physiological and behavioral data. This work was carried out in part by Robert W. Steer, Jr., in partial fulfillment of the requirements for the degree of Doctor of Science, granted by M.I.T. in August 1967. The degree to which our objectives were realized is outlined as follows.

Physical Properties of the Labyrinthine Fluids

The properties of viscosity, thermal coefficient of viscosity, density, and thermal coefficient of expansion were measured for endolymph and perilymph and were used to evaluate the coefficients of the equations of the dynamic response of the semicircular canals. These measured properties and the measurement accuracies are presented in MV-67-2.

A microviscometer was designed, built, and calibrated for use on 1-2 microlitre fluid samples. The design and operational procedures of the microviscometer and sample handling techniques are also presented in MV-66-2 and MV-67-2.

Canalicular Response to Angular Acceleration and Rotation in a Linear Acceleration Field

Hydromechanical analysis of the semicircular canals as a rigid torus filled with fluid and subjected to a constant angular acceleration showed that the damping to inertia ratio

of the canalicular duct was an order of magnitude higher than is calculated from the observed objective and subjective responses of man to angular accelerations. Investigation of the influence of viscous drag of the cupula on the membranous ampulla showed that for the dimensions of the cupula and the clearance between the cupula and the ampulla that is observed from histological studies, the cupula drag contributes as much damping to the semicircular canals as the hydrodynamic drag of endolymph in the canalicular duct. Further, the moment of inertia of the cupula and the endolymph adjacent to it in the ampulla is shown to be an order of magnitude greater than the inertia ring of the endolymph in the canalicular duct. [These results resolve the disparity between the calculated and observed dynamic responses of the semicircular canals. Further, they indicate that the elasticity, viscous drag, and inertia of the cupula are the principal determinants of these dynamic properties with the endolymph-filled duct providing some damping but acting primarily as an inertia ring to sense angular acceleration and pump the endolymph into the ampulla] (see MV-67-2).

Further examination of the structure of the membranous canal duct showed it to be flexible, denser than the surrounding endolymph and perilymph, and attached by fibrous connections along its outer periphery to the bony canal. The distension of the duct under the influence of linear acceleration, which acts on the density differences between the duct and the fluids, was shown to be responsible for a "roller pump" action when the canal is rotated about an axis

orthogonal to the linear acceleration field. This roller pump action produces a steady state cupula deviation in response to a constant rotation in an acceleration field and offers a realistic physical explanation for the observed bias component of neural discharge from cat canalicular neurons when the animals are subjected to counter-rotating motion. We have shown that less than a 3%/g constriction in duct cross-sectional area can produce the bias component of vestibular nystagmus that has been observed in experiments where the subjects were constantly rotated about a horizontal longitudinal axis, experiments where subjects were rotated about a vertical axis in a lateral acceleration field by use of a rotating chair mounted on the boom of a centrifuge, and in experiments showing the analysis of the bias component of rotary nystagmus observed from dynamic counterrolling (see MV-67-3).

This canalicular response to rotation in a linear acceleration field is of some consequence in that it gives the human a significant vestibular input of the same physiological character as angular acceleration. If rotating environments are to be used for gravity simulation or space station stabilization, then man's ability to interpret correctly and to adapt to this new vestibular information must be carefully considered.

Canalicular Response to Thermal Stimulation

Caloric stimulation was shown to produce the physiological equivalent of an angular acceleration. A torque is

induced on the endolymph as the result of a temperature gradient across the lateral semicircular canal when the external auditory meatus is irrigated with water at a temperature different from normal body temperature. Analysis of the published results of previous researchers, who measured the time history of the temperature gradient across the lateral canal due to caloric irrigation, produced a system transfer function description relating the temperature of irrigation to an equivalent angular acceleration. It is of the form of a first order lag with a 25 second thermal lag and a gain constant that is consistent with the ratio of the threshold levels of caloric and angular acceleration stimulations. The time history of cupula displacement calculated by cascading the thermal lag transfer function with the hydrodynamic transfer function of the canal was shown to be in close agreement with the time history of the slow phase velocity of caloric vestibular nystagmus. Our experiments to evaluate the latency time to the onset of caloric vestibular nystagmus confirm the computed functional relationship and show it to be analogous to the Muelder product which relates the latency time to the onset of subjective sensation of rotation and the strength of angular acceleration stimulation (see MV-66-2 and MV-67-2).

In summary, the results of this investigation have yielded new information on the physical properties of the labyrinthine fluids. The influences of the inertia and viscous drag of the cupula and of the flexible membranous canalicular duct have resulted in a new dynamic model for the response of

the semicircular canals to angular and linear acceleration. Further, the demonstrated physiological equivalence between caloric stimulation and angular acceleration now permits inclusion of caloric stimulation in this description of the sensory capabilities of the semicircular canals.

II. FUTURE PLANS

The Man-Vehicle Laboratory performs research in areas relating to the limitations and capabilities of men involved in guidance, control, and stabilization of moving vehicles. In keeping with the objectives of the Man-Vehicle Laboratory, we will develop a quantitative description for the control of posture in the human. Since posture control demonstrates a primary use of the motion sensors, the study represents the logical application of the vestibular research recently completed by the laboratory.

A detailed investigation of human neurophysiology and anatomy related to posture control will culminate in a model applicable to further research in engineering and medicine. The direct engineering application for this model will be in determining the feasibility of using postural rather than manual control of moving vehicles.

The interaction of the various components in the posture control model is shown in Fig. 1. The control of posture is presented here as the interaction of feedback information on two levels:

1. The lower level reflex control involving the muscle spindle sensors and involuntary commands emanating from the spinal level only.
2. The upper level control involving the integration of motion and position information in the brain and resulting in both voluntary and involuntary commands to the motoneurons and to the muscle spindle receptors.

Since reflexes can account only for partial stability, the higher level controls are necessary for complete stability. The optimal interaction of these two loops (over a wide range of disturbance conditions) is possible through the adaptability of the reflex characteristics.

The areas of interest to be emphasized in the initial research will be:

1. The description of the role of each muscle and receptor group in the control of posture.
2. The complete description of the range of reflex control characteristics.
3. The interaction of reflex control with the higher level control under varying disturbance conditions.

Our research will concentrate on the description of the flow of information, both in the lower level reflex loops and in the higher level patterned responses. The postural control model will demonstrate the functional importance of each muscle and receptor group in the overall control task. The model will also include a description of the use of the higher senses including vision, motion (vestibular), and touch, in the

maintenance of posture. Since a general attack on the posture control problem is a broad and multi-dimensioned one, our study will concentrate on the specific case of a man standing erect in a fixed position with his feet together. The finer resolution of control functions that is possible in the study of this constrained case will indicate many of the control patterns to be expected in a more complete posture control description.

The choice of a simplified posture control task is necessary to maintain the description of the information paths and the definition of the component functions on a workable level. The interaction of the different levels of control can be observed quantitatively only in the absence of interference from the very complex learned responses such as stepping and hopping.

One of the primary experimental goals of the research will be to determine the relative roles of the reflex and higher level controls in the maintenance of posture. Continuous measurement of the joint angles and reaction torques for the joints are necessary to describe quantitatively all of the posture responses. To describe adequately the reflex response, a method for measuring the stiffness of the ankle joint will be developed. The differentiation of the reflex response from the higher level response is possible if a quantitative measure of the total response and of the joint stiffness are both known as continuous functions of time.

The primary method for observing this interaction of the different levels of control will be the use of a platform instrumented to diminish or augment the characteristics of the reflex loop with a minimum of interference to the responses

of the higher centers. Experiments with the subject under varying degrees of sensory deprivation will also be used to affect the characteristics of the higher level controls. Specific postural control tasks including standing without disturbance, maintaining balance under lateral accelerations, and maintaining balance in the presence of a pitching floor will be investigated. This phase of our work is being carried out in cooperation with orthopedic surgeons and neurophysiologists at the Harvard Medical School.

III. PUBLICATIONS

The following two theses have been completed in the Man-Vehicle Laboratory through the support of this grant.

The Influence of Angular and Linear Acceleration and Thermal Stimulation on the Human Semicircular Canal

by

Robert W. Steer, Jr.

Abstract

The hydrodynamic properties of the human semicircular canal system were studied to determine its dynamic characteristics and their relationship to observed subjective and objective vestibular responses to various motion inputs. Four topics of particular importance in current vestibular research were examined in detail.

The density, coefficient of expansion, and viscosity of the labyrinthine fluids, endolymph and perilymph, have been measured to provide precise values for the coefficients of the dynamic models. A microviscometer was designed, built, calibrated, and used to measure the viscosity of 1-2 microlitre samples of endolymph and perilymph. Density measurements were made via precision balance scales and accurate volume measurements and coefficients of expansion were made by microscopic measurements of the volume of the fluids at several temperatures.

The semicircular canal is modelled as a rigid torus of fluid, with the cupula acting as an elastic and viscous restraint. A system transfer function is evaluated for cupula displacement as a function of angular acceleration. It is shown that the cupula's viscous drag on the wall of the membranous labyrinth accounts for the majority of the damping in the system and resolves the disparity between previous calculations of damping, which only considered the hydrodynamic drag of endolymph in the canalicular duct and measured damping coefficients.

Caloric stimulation of the vestibular apparatus is examined, and a model is proposed based on the published measured time history of the temperature gradient across the lateral canal when the external auditory meatus is irrigated with water above or below body temperature. The presence of a thermal gradient across the lateral canal is shown to produce the physiological equivalent of an angular acceleration because of the torque which acts on the endolymph as a result of its thermal coefficient of expansion. Caloric experiments were performed which attest to the validity of the model.

The influence of linear acceleration on the semicircular canals was investigated. Human objective and subjective responses to rotation about a horizontal axis, to counter-rotation, and to stimulation by a rotating acceleration vector were examined. The observed responses of long duration nystagmus and continuous sensation of rotation are not in conformity with classical models of the vestibular system and there has developed a sizable body of experimental evidence which attributes a significant portion of these unusual responses to the semicircular canals. It is shown through the distensibility of the canalicular duct under the influence of linear acceleration, that the observed bias component of nystagmus can be attributed to a first order nonlinearity of the semicircular canal dynamics. Experiments were performed on a centrifuge equipped with a rotating chair to show the relationship between the magnitude of the acceleration field, the rotation rate of the subject, and the slow phase velocity of vestibular nystagmus.

Perception of Rotation - Nystagmus and Subjective

Response at Low Frequency Stimulation

by

Gerald B. Katz

Abstract

A rotating chair was built to submit subjects to sinusoidal angular accelerations at various combinations of frequencies (.01 cps to .1 cps) and peak angular acceleration levels ($10^\circ/\text{sec}^2$ to $45^\circ/\text{sec}^2$), for the purpose of studying the human subjective and objective response to rotation at low frequencies. Each

of four subjects was seated in the completely dark chair with the axis of rotation passing through his head.

His subjective response was measured by means of a directional switch; his objective nystagmus eye movement response was simultaneously measured and recorded. A study of the resultant phase differences between both subjective and objective perceptions of angular velocity and actual angular velocity leads to the following conclusions:

1. The phase lead of both objective and subjective response exhibited no simple functional dependence upon amplitude of acceleration.
2. The amount of phase lead in both cases is inversely proportional to stimulus frequency.
3. The objective phase lead is larger at any stimulus condition than the corresponding subjective phase lead.
4. Intersubject response differences were very evident, irregular, and relatively great.
5. The data presented agrees in a gross manner with the data of Hixon and Niven.

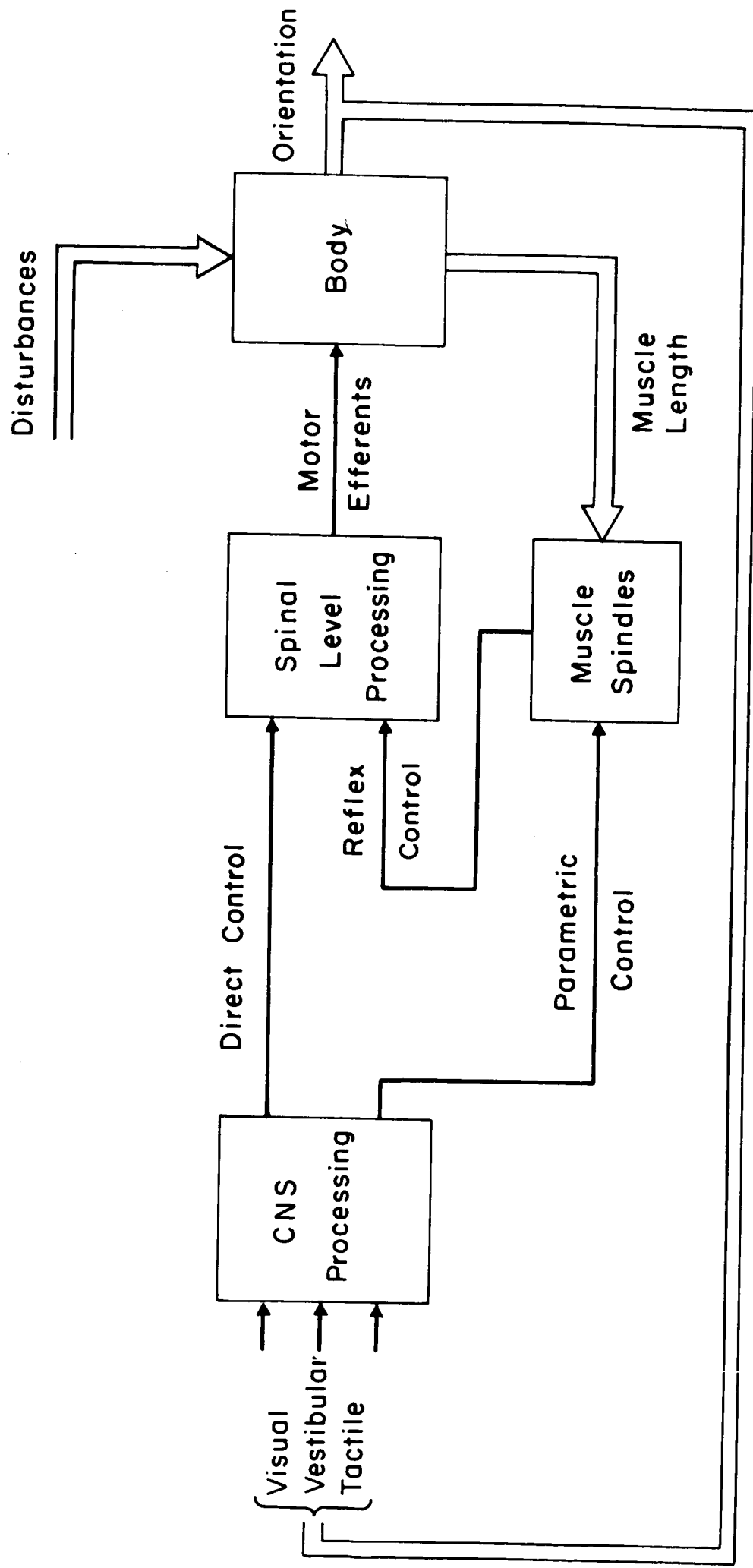


Fig. 1. The posture control model